

# EVIDENCE FOR AN INDO-PACIFIC ORIGIN OF HAWAIIAN ENDEMICS IN *BALCLUTHA* AND RELATED GENERA (CICADELLIDAE: MACROSTELINI)

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**ABSTRACT.**—The 10 endemic species of *Balclutha* in Hawaii are reviewed and compared with the Pacific and American forms of the genus. Two new species, *nigricentris* and *fuscifrons*, are described; *kilaueae* is transferred to a new genus *Balolina* n. comb.; *beardsleyi* is synonymized with *saltuella*, n. syn.; and *hospes* is relegated to a subspecies of *incisa*, n. stat. Descriptions and notes, together with illustrations and a key, are given for each taxon. Evidence is presented to suggest that all the endemic species of *Balclutha* have arisen within the islands from a single colonization and that the taxon showing the greatest similarity to them is the widespread Pacific species *B. lucida*. It is shown that the Hawaiian genus *Nesolina* is most closely related to the endemic species-group of *Balclutha* and that *Balolina* is an independent colonization.

The isolated position, volcanic origin, and diverse habitats of Hawaii, together with the division of the area into several large islands, have combined to produce a depauperate, yet large and highly endemic, biota (Simon 1987). This phenomenon is well illustrated by the plant-feeding insect family Cicadellidae. The family was studied in the islands by Kirkaldy (1910) and Osborn (1935) and subsequently reviewed by Zimmerman (1948). Namba (1956) later described several new species.

In his review of the Hawaiian insect fauna, Zimmerman (1948) considered the generic affinities to be predominantly Pacific and only 5% American. The Homoptera were considered to be exclusively Pacific, although little evidence was provided.

Compared with the Pacific and mainland America, the Hawaiian cicadellid fauna is very depauperate at the supraspecific level. Only 5 of the 35 subfamilies are present, 4 of which are represented by 5 recently introduced species from North America. In contrast, the Deltocephalinae, a large, worldwide group with 17 currently recognized tribes, is represented by 2 tribes. The endemic genera *Nesophryne* (2 species), *Kirkaldiella* (2 species), and *Nesophrosyne* (60 species) belong to the Opsiini and are related to the Pacific genus *Orosius* (Linnavuori 1960, Ghauri 1966). *Nesolina* (1 species), *Balolina* n. gen. (1 species), and the cosmopolitan genus *Balclutha*, comprising 105 species and represented in Hawaii by 11 endemic and 2 cos-

mopolitan species, belong to the Macrostelini, the major cicadellid group in the similarly isolated islands of Marquesas in the Pacific, and St. Helena in the Atlantic. This tribe contains approximately 30 genera worldwide, of which 10 are island endemics, 2 in Hawaii, 4 in the Marquesas, and 4 on St. Helena. Interestingly, although the main host plants of the group are Gramineae, in Hawaii, Marquesas, and St. Helena shrubs and tree ferns of southern temperate distribution are also utilized (Webb 1987).

## MATERIALS

The material studied is primarily from the Bishop Museum, together with some in the British Museum (Natural History), abbreviated throughout the text to BPBM and BMNH, respectively.

## METHODOLOGY

The present study investigates the origins of the Hawaiian *Balclutha* species. This has necessitated a reexamination of all the Hawaiian species and a review of the variation in characters among Pacific and American species of the genus. Until a phylogenetic analysis of the genus and tribe is undertaken, any statements on the polarity of characters within these taxa would be premature. Our biogeographical inquiry is therefore based on phenetic resemblances rather than on shared

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apomorphies and should be seen as only exploratory and preliminary in nature.

#### FAUNAL RELATIONSHIPS OF HAWAIIAN *BALCLUTHA*

The variation in morphological characters in *Balclutha* was reviewed by Knight (1987) for the south and west Pacific species and by Blocker (1967) for the American species. Both faunas are of comparable size, 30 and 32 species, respectively, but have only 3 species in common, *saltuella*, *incisa*, and *lucida*.

Compared with the Pacific and American species, the 10 endemic Hawaiian species, *nigriventris* n. sp., *fuscifrons* n. sp., *grandis* Namba, *phoxocephala* Namba, *timberlakei* (Osborn), *lobata* Namba, *usitata* Namba, *volcanicola* (Kirkaldy), *plutonis* (Kirkaldy), and *peregrina* (Kirkaldy), differ only slightly from each other in head shape and minor details of the male genitalia, suggesting that they probably arose from one founder species. The character states common to the 10 endemic species are listed below, the condition present in the 10 endemic species shown in italics:

1. Relative width of head and pronotum: *head equal to or wider than the pronotum.*
2. Length of vertex: *longer medially than next to eyes.*
3. Laterofrontal sutures: *terminating at or near the ocelli.*
4. Distance between ocelli and eyes: *ocelli separated from the eyes by a distance equal to 2–4 times their own diameter.*
5. Foretibia setal formula: *1.3.*
6. Hind femora setal formula: *2.1.1.*
7. Shape of male pygofer: *simple, without ventral lobes or processes.*
8. Shape of subgenital plates: *triangulate, with apical, fingerlike process 1/4–1/2 total length of plate.*
9. Shape of styles: *robust, with apical process and preapical lobe well developed.*
10. Relative length of stem and arms of connective: *stem longer than arms.*
11. Shape of aedeagal shaft: *simple, elongate, curving dorsally or anterodorsally to point level with or slightly anterior to atrium.*

#### Comparison between the Hawaiian, Pacific, and American Species

In the present section, the Pacific and American species of the genus are reviewed for each of the characters listed above. The alternative conditions of characters 3, 5, and 7 are coded A and B for ease of reference in

subsequent discussion.

The relative width of the head (character 1) varies within the genus and may be wider, equal to, or narrower than that of the pronotum. All three conditions are present in both the American and the Pacific faunas, half the species in each region showing the head approximately equal to or wider than the pronotum, as in Hawaii.

The vertex (character 2) is usually short and uniform in length and is one of the main distinguishing features of the genus. The medial prolongation of the vertex found in the Hawaiian species occurs in the Pacific in only *smaragdula*, and in a few individuals of *flagellata*, *bifasciata*, *rieki*, and the cosmopolitan species *punctata*. It is far more prevalent among the American forms, being a characteristic feature of 7 species and occurring occasionally in 15 others.

The laterofrontal sutures (character 3) usually terminate at or near the ocelli (condition B) but are occasionally turned medially, ventrad of the ocelli (condition A). With the exception of *simplex* and the cosmopolitan *saltuella*, the Pacific species have the sutures terminating near the ocelli as in Hawaiian species. Both conditions also occur in the American fauna but with an approximately equal number of species of each.

The ocelli (character 4) are usually small and situated on the anterior margin of the head, separated from the corresponding eye by approximately their own diameter. Most of the American and Pacific species have the ocelli in this position, or only slightly more remote from the eye. Only *impicta* and *arctica* in America, *flagellata* and *cheesmanae* in the Pacific, and the cosmopolitan species *punctata*, have the ocelli more than twice their own diameter from the eyes, and approximating the condition found in Hawaiian species. The Pacific fauna shows greater flexibility in this character, however, with *chloroptera* and *bulbosa* having the ocelli enlarged and more dorsad in position.

Throughout the genus, the foretibia setal formula (character 5) may be 1.1 (condition A), 1.3 (condition B), or rarely 1.4. The condition in Hawaii (condition B) is similar to that in the majority of Pacific species. Only two Pacific species, *simplex* and the cosmopolitan *saltuella*, show condition A. In the American fauna, half of the species examined have condition A and half condition B.

The setal pattern at the apex of the hind femora (character 6) varies within the genus from 2.1.1 to 2.2.1. The two conditions occur equally throughout both the Pacific and American faunas, unlike Hawaii where only the former is found.

The male pygofer (character 7) varies from a simple, rounded shape (condition A), as found in Hawaii, to a more complex form with posteroventral lobes or processes (condition B). The simple form is rare outside Hawaii, occurring in only *simplex* in the Pacific and in the species *lucida* and *saltuella*, which occur in both regions.

The subgenital plates (character 8) are characterized in all species by a membranous, fingerlike, apical segment. The shape of the plate found in the Hawaiian species occurs in the majority of Pacific and American species, being slightly more prevalent in the latter region. The remaining species in both regions have the basal part of the plate much reduced in size.

The robust, well-developed styles (character 9) of the Hawaiian species occur in the majority of species in both the Pacific and America but are more widespread in the former. Only two Pacific species, *bulbosa* and *rieki*, have a reduced style, compared with nine species in the Americas, plus the cosmopolitan *saltuella* in both regions.

The Y-shaped connective (character 10) varies principally in the relative length of the stem and arms. The condition present in Hawaii, with the stem longer than the arms, is present in 50% of the species in the Pacific but in only 30% of the species in America.

A simple, filamentous aedeagus (character 11) is characteristic of the majority of species in the genus. In the Hawaiian species the shaft is directed dorsally or curved anterodorsally to a point approximately level with the well-developed, basal apodeme, a form that occurs in 50% of the fauna in both the Pacific and America.

#### Faunal Similarity

If we take the number of species in each region showing character states identical with those in Hawaii as a measure of similarity, then the Hawaiian species show greater similarity to the Pacific fauna with respect to the laterofrontal sutures, foretibial setal pattern, styles, connective, and to a lesser extent the

ocelli and male pygofer. The American species show greater similarity only in the length of the vertex and to a lesser extent in the shape of the subgenital plates. The relative width of the head, the setal pattern on the hind femora, and the shape of the aedeagus provide little information in this respect. If we eliminate those characters that confer only minimal regional preference, such as the ocelli, male pygofer, and subgenital plates, and also those known to vary infraspecifically, such as the length of the vertex, we are left with only four, the laterofrontal sutures, the foretibial setal pattern, and the shape of the styles and connective, all of which support the theory of closer links with the Pacific.

Further support for a Pacific link is provided by the Sorensen Coefficient of Similarity (Southwood 1978)

$$Cs = 2j/(a + b)$$

where  $j$  is the number of character states common to the two areas and  $a + b$  are respectively the number of character states in each area. Based on the endemic species in each area, the coefficient for Hawaii and the Pacific is 0.74 and for Hawaii and the Americas is 0.58, showing a greater degree of similarity between the first two areas.

From the above review it is seen that no one character is shared exclusively between Hawaii and either of the other two regions to provide evidence of affinity. However, if we consider a combination of characters, rather than single characters alone, then the picture becomes a little clearer.

Table 1 shows the Pacific species and their similarity or dissimilarity to the Hawaiian endemic species with regard to the 11 characters. This reveals an obvious correlation between characters 3, 5, and 7. All three characters show condition A<sup>2</sup> in the first two species and condition B<sup>2</sup> in the fourth species onward. An intermediate stage occurs in the third species, *lucida*, which has condition B in characters 3 and 5 but retains condition A in character 7. The American species show the same correlation between characters 3, 5, and 7, but, except for *lucida*, the character states in the intermediate stage are reversed. This is shown in Table 2, where the intermediate stage is highlighted for each region. The similarity between the Hawaiian endemics and *lucida* in this respect is unique.

<sup>2</sup>See previous section, paragraphs 4, 6, and 8.

TABLE 1. A list of the Pacific species of *Balclutha*, showing the similarities (+) and differences (–) between them and the Hawaiian endemics for the 11 listed characters. (For further explanation, see text.)

Pacific species	Characters										
	1	2	3	4	5	6	7	8	9	10	11
<i>saltuella</i>	+	–	–	–	–	+	+	–	–	–	+
<i>simplex</i>	+	–	–	–	–	+	+	–	+	–	+
<i>lucida</i>	+	–	+	–	+	+	+	+	+	–	–
<i>bilobata</i>	–	–	+	–	+	+	–	–	+	–	–
<i>batuensis</i>	+	–	+	–	+	–	–	+	+	+	+
<i>punctata</i>	–	±	+	+	+	–	–	+	+	+	+
<i>neglecta</i>	+	–	+	–	+	+	–	+	+	–	+
<i>viridinervis</i>	+	–	+	–	+	–	–	+	+	±	–
<i>flagellata</i>	–	±	+	+	+	–	–	+	+	±	–
<i>bifasciata</i>	+	±	+	–	+	+	–	–	+	+	+
<i>trilineata</i>	±	–	+	–	+	–	–	+	+	–	–
<i>rieki</i>	+	±	+	–	+	+	–	–	–	–	+
<i>cheesmanae</i>	–	–	+	+	+	–	–	+	+	+	–
<i>yanchepeensis</i>	±	–	+	–	+	–	–	+	+	+	+
<i>smaragdula</i>	–	+	+	+	+	+	–	–	+	+	+
<i>alstoni</i>	+	–	+	–	+	–	–	+	+	+	+
<i>kuroiwae</i>	+	–	+	–	+	?	–	–	+	+	+
<i>asymmetrica</i>	–	–	+	–	+	?	–	+	+	–	–
<i>chloroptera</i>	–	–	+	±	+	–	–	+	+	+	–
<i>bulbosa</i>	–	–	+	±	+	–	–	+	–	+	–
<i>bacchusi</i>	+	–	+	–	+	+	–	+	+	+	+
<i>spiniloba</i>	+	–	+	–	+	?	–	+	+	+	+
<i>incisa</i>	+	–	+	–	+	+	–	+	+	+	–
<i>rosea</i>	+	–	+	–	+	+	–	+	+	–	+
<i>pseudorosea</i>	+	–	+	–	+	+	–	+	+	–	+
<i>rubrostriata</i>	+	–	+	–	+	+	–	+	+	+	+
<i>wilsoni</i>	–	–	+	–	+	–	–	+	+	–	–
<i>distenda</i>	–	–	+	–	+	–	–	+	+	–	–
<i>rubrinervis</i>	–	–	+	–	+	–	–	+	+	–	–
<i>noonadana</i>	±	–	+	–	+	–	–	+	+	–	–

TABLE 2. Character-state distribution for three characters in Pacific and American species of *Balclutha*. (For further explanation, see text.)

Pacific species	Characters			American species*	Characters		
	3	5	7		3	5	7
<i>saltuella</i>	A	A	A	<i>saltuella</i>	A	A	A
<i>simplex</i>	A	A	A				
<i>lucida</i>	B	B	A	<i>neglecta</i>	A	A	B
				<i>chiasma</i>	A	A	B
				<i>sandersi</i>	A	A	B
remaining spp.	B	B	B	remaining spp.	B	B	B

\**lucida*, which occurs in Central and South America, has been omitted from this half of the table in the interests of clarity.

Distribution of *B. lucida*

Since *lucida* is the species most similar to the Hawaiian forms, it is of interest to examine its distribution relative to Hawaii. Figure 53 shows its distribution, extending from the Aldabra Islands (Webb 1980 [*filum*]) in the west to Central and South America in the east (Blocker 1967 [*floridana*] and Knight 1987). It is a tropical and semitropical species clearly

capable of movement over long distances and with the ability to colonize and establish itself on islands and mainland areas. Its presence in the Marshall and Marquesas islands places it within a comparatively short distance from Hawaii. The available data, however, provide no information on the center of origin for the species, although its absence from mainland Africa and Asia suggests that it is either the Pacific or Central America.



# RELATIONSHIP OF *BALCLUTHA* TO OTHER HAWAIIAN MACROSTELINI

In addition to *Balclutha*, two other macrosteline genera occur in Hawaii, both endemic.

The monotypic genus *Nesolina* differs from *Balclutha* principally in the more elongate head and the possession of longitudinal brown stripes on the vertex and pronotum. In all other characters it closely resembles the endemic species of *Balclutha* to which it is probably most closely related. Despite this close similarity, the present status of *Nesolina* is preserved, pending a phylogenetic study of the Macrostelini.

The relationship of the remaining Hawaiian macrosteline genus, *Balolina* n. gen., is uncertain. Although it is similar in general appearance to *Balclutha* and the Pacific genus *Nesoclutha* and has the first valvulae fused as in *Balclutha* (Fig. 33), it differs in many significant features, as listed below in the key and generic description. Except for the position of the ocelli, there is little to indicate that it is in any way related to the Hawaiian species of *Balclutha*. On the contrary, it appears to be an independent introduction to the islands.

All three Hawaiian macrosteline genera belong to a group having the hindwing veins sc and r united into a single vein, with a consequent reduction in the number of apical cells (Fig. 32). This is considered by Ossianilsson (1983) to be justification for placing *Balclutha* in a separate tribe, the Balcluthini, which is also characterized (Oman 1949) by the possession of a sulcate hind basal tarsus (Fig. 74). Both characters are found to some degree, however, in other genera, including *Macrosteles*. The phylogeny of the Macrostelini proposed by Triplehorn and Nault (1985) includes *Balclutha* but omits several other genera, including the 10 island endemics. Some of these have been treated by Webb (1986, 1987).

## DISTRIBUTION OF HAWAIIAN MACROSTELINI

Table 3 summarizes previous (x) and new (N) distribution data and shows that the largest and youngest islands, Hawaii and Maui, respectively, support the most species, and that Kauai and Molokai, which differ considerably in size, have similar numbers of species. Further collecting on the islands may

have profound effects on the distributional records and may even reveal further species.

## KEYS AND DESCRIPTIONS

The taxonomy of the Hawaiian Macrostelini has been treated by several authors (see introduction), but descriptions are usually incomplete and contain little information on intraspecific differences. Namba's (1956) revision of *Balclutha* was a considerable improvement on previous work, but a few of the characters referred to are unreliable. New keys to genera and species are given to take account of this and to accommodate the new taxa. All host records given below are taken from either Zimmerman (1948), Namba (1956), or specimens examined.

### Key to the Genera of Hawaiian Macrostelini

1. Head and thorax with longitudinal, brown bands; vertex elongate (Fig. 54) . . . . . *Nesolina*
- Head and thorax not marked as above; vertex short to moderately long (Figs. 7, 15) . . . . . 2
- 2(1). Vertex moderately long, ocelli situated almost to point midway between eye and midlength of foremargin of vertex (Fig. 67). Clypeus extending well beyond margin of face, trans-clypeal suture obscure; laterofrontal sutures short (Fig. 68). Foretibia with apical setae similar in length (Fig. 73). Hind femur with apical setal formula 2+2+1 (Fig. 69). Macrosetae of legs and genital segment nonhairy. Aedeagal shaft with pair of apical processes (Fig. 82); gonopore apical on ventral surface (Fig. 76). Connective with stem very short (Fig. 80). Subgenital plate with irregular macrosetae (Fig. 83). Second valvulae evenly tapered to apex; teeth extending over distal half of dorsal margin and onto apex of ventral margin (Fig. 75) . . . . . *Balolina*
- Vertex short to moderately long; ocelli situated near eye or at point one-third distance from eye to midlength of foremargin of vertex (Figs. 2, 15, 28). Foretibia with apical setae dissimilar in length (Fig. 35). Hind femur with apical setal formula 2+1+1 (Fig. 30). Male and female genitalia not as above . . . . . *Balclutha*

### Key to Species of Hawaiian *Balclutha*

1. Vertex of uniform length; ocelli 1.0–1.5 times own diameter from corresponding eye; coronal suture visible in facial view (Figs. 28, 29) Pygofer lobe with a ventral process (Figs. 37, 46). Connective with arms equal in length to stem (Fig. 42) . . . . . 11
- Not as above . . . . . 2
- 2(1). Yellow to greenish yellow, marked with brown on first thoracic sternite (as in *saltuella*, Fig.

TABLE 3. Distribution of the Macrostelini on the Hawaiian islands, from the oldest in the north (left) to the youngest in the south (right).

Area (sq km)	Kauai 1437	Oahu 1564	Molokai 673	Lanai 365	Maui 1885	Hawaii 10437
<i>Nesolina</i>						
<i>lineata</i>	—	x	—	—	—	x
<i>Balolina</i>						
<i>kilaueae</i>	x	x	x	—	x	x
<i>Balclutha</i>						
<i>grandis</i>	x	—	—	—	—	—
<i>saltuella</i>	—	x	—	—	—	—
<i>phoxocephala</i>	x	x	x	—	—	—
<i>incisa hospes</i>	x	x	x	x	x	x
<i>timberlakei</i>	N	x	x	x	x	x
<i>lobata</i>	x	x	N	—	x	x
<i>usitata</i>	x	x	N	—	x	x
<i>volcanicola</i>	—	—	x	—	N	x
<i>plutonis</i>	—	—	—	—	x	x
<i>peregrina</i>	—	—	—	—	x	x
<i>nigriventris</i>	—	—	—	—	N	N
<i>fuscifrons</i>	—	—	—	—	N	—
Total	7	8	7	2	10	11

- 43), abdomen (at least dorsally), and sometimes legs . . . . . 3

— Not marked as above or if abdomen and first thoracic sternite marked with brown, then overall color yellow tinged with scarlet . . . . . 5

3(2). Large species, 4.0–4.4 mm in length. Aedeagus and style as in Figures 3, 4, 18 . . . . . *fuscifrons*, n. sp.

— Small to moderately large species, up to 3.5 mm . . . . . 4

4(3). Vertex marked with stramineous or brown (Figs. 5, 7). Aedeagal shaft robust (Fig. 24) . . . . . *volcanicola* (Kirkaldy)

— Vertex without markings. Aedeagal shaft slender (Fig. 19) . . . . . *nigriventris*, n. sp.

5(2). Large species 4.5–5.3 mm in length. Stem of connective broad. Aedeagus as in Figure 21 . . . . . *grandis* Namba

— Small to moderately large species, up to 4.0 mm . . . . . 6

6(5). Preapical lobe of style large; apical process abruptly tapered distally (Figs. 16, 17). Female genital sternite marked with brown on disc (Fig. 8) . . . . . *lobata* Namba

— Not as above . . . . . 7

7(6). Moderately large species, 3.5–4.0 mm. Clypellus with sides concave. Connective elongate, longer than style (as in *timberlakei*, Figs. 13, 14). Aedeagal shaft slender, evenly curved dorsally (Figs. 25, 26) . *plutonis* (Kirkaldy)

— Small species, 2.6–3.1 mm; without the above combination of characters . . . . . 8

8(7). Aedeagal shaft slender (Figs. 25, 27) . . . . . 9

— Aedeagal shaft robust (Figs. 22, 23) . . . . . 10

9(8). Clypellus with sides straight (Fig. 12). Aedeagal shaft evenly curved throughout length (as in
- plutonis*, Fig. 25) . . . . . *peregrina* (Kirkaldy)

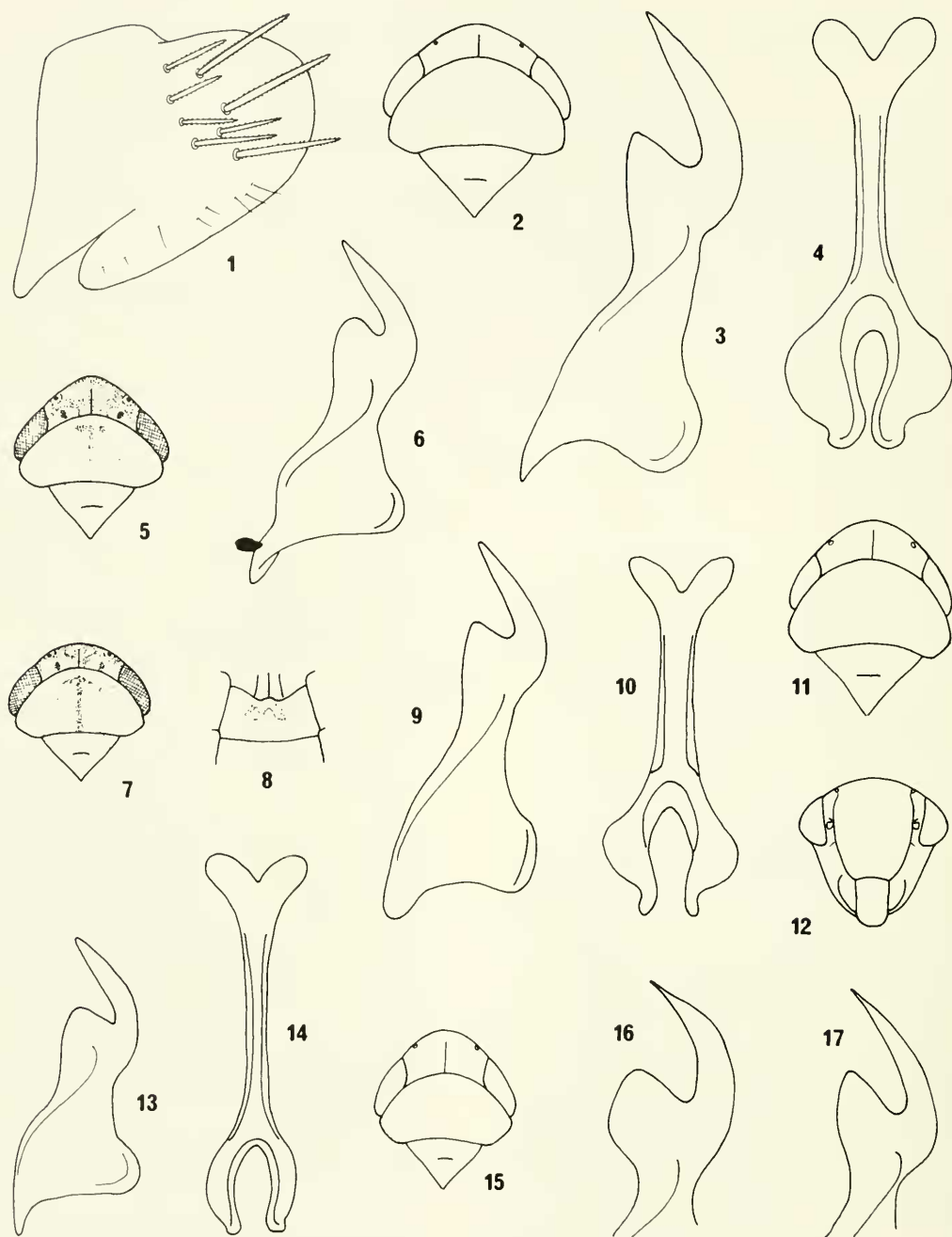
Clypellus with sides concave. Aedeagal shaft angularly curved basally (Fig. 27) . . . . . *usitata* Namba

10(8). Aedeagal shaft sinuate (Fig. 22). Connective elongate, longer than style (Figs. 13, 14) . . . . . *timberlakei* (Osborn)

— Aedeagal shaft not sinuate (Fig. 23). Connective approximately equal in length to style . . . . . *phoxocephala* Namba

11(1). Female pregenital sternite with disc marked with brown (Fig. 36). Male genitalia as in Figures 37–40 . . . . . *incisa hospes* (Kirkaldy)

— Female pregenital sternite not marked with brown. Male genitalia as in Figures 41, 42, 45, 46 . . . . . *saltuella* (Kirschbaum)
- Balclutha* Kirkaldy
- Balclutha* Kirkaldy, 1900: 243. New name for *Gnathodus* Fieber, 1866; Blocker 1967: 4, Knight 1987: 1178. Type species: *Cicada punctata* Fabricius, 1775, by monotypy.
- Balclutha fuscifrons*, n. sp.  
Figs. 1–4, 18
- LENGTH.—♂, 4.0–4.2 mm; ♀, 4.2–4.4 mm.  
Yellow tinged with green, abdomen heavily marked dorsally and ventrally with dark brown; clypeus pale to dark brown; legs and thoracic sternites variably marked with dark brown.  
Head approximately equal in width to pronotum. Vertex with medial length approximately 1.33 times length next to eye. Ocelli marginal, separated from corresponding eye by distance equal to 3–4 times own diameter.



Figs. 1-17. Endemic Hawaiian *Balchutha* species. 1-4, *B. fuscifrons*: 1, male pygofer, left lateral view; 2, head and thorax, dorsal view; 3, right style, dorsal view; 4, connective, dorsal view. 5-7, *B. volcanicola*: 5, head and thorax, dorsal view (Kilauea); 6, right style, dorsal view; 7, head and thorax, dorsal view (Wailua). 8, *B. lobata*, female pregenital sternite. 9-11, *B. nigriventris*: 9, right style, dorsal view; 10, connective, dorsal view; 11, head and thorax, dorsal view. 12, *B. peregrina*, face. 13-15, *B. timberlakei*: 13, right style, dorsal view; 14, connective, dorsal view; 15, head and thorax, dorsal view. 16-17, *B. lobata*, apex of right style, dorsal view.

Face slightly wider than long; clypellus with sides concave, apex extending very slightly beyond margin of face; laterofrontal sutures

convex, distally concave, reaching to corresponding ocellus. Setal formulae: foretibia, 1.3 or 1.4; midtibia, 4.3, 4.4, 5.3, or 5.4; hind

femur, 2.1.1 or 2.1.1.1.

MALE.—Pygofer simple, posterior margin broadly and evenly rounded in lateral aspect. Subgenital plate tapered distally to moderately long, fingerlike process. Connective with arms shorter than stem. Style approximately equal in length to connective, preapical lobe elongate. Aedeagal shaft slender, more or less straight distally.

FEMALE.—Pregenital sternite with posterior margin more or less straight. Valvulae as in *incisa* (Figs. 33, 38).

HOST.—Unknown.

DISTRIBUTION.—Endemic (Maui).

HOLOTYPE.—♂, Maui, Kula Pipe Line, 4,200', vii.1956, R. Namba (BPBM). Paratypes: Maui: 13♂, 19♀, same data as holotype; 4♂, Holua, Haleakala Crater, vi.1983, D. E. Hardy; 4♂, 9♀, Waikamoi, 4,000', D.E. Hardy (BPBM, BMNH).

REMARKS.—This species can be distinguished by its large size, brown markings, and more or less straight aedeagal shaft. Its external appearance is similar to *Balolina kilaueae*, with which it may be confused.

*Balclutha volcanicola* (Kirkaldy)

Figs. 5–7, 24

*Nesoteles volcanicola* Kirkaldy, 1910: 574; Osborn 1935: 58, Fig. 24e. Lectotype ♂, Hawaii (BPBM), here designated [examined].

*Balclutha volcanicola* (Kirkaldy): Zimmerman 1948: 87, Fig. 27, Namba 1956: 107–108, Fig. 7.

HOST.—*Cyperus* (Cyperaceae), *Eragrostis* (Gramineae), *Lythrum* (Lythraceae).

DISTRIBUTION.—Endemic (Molokai, Maui, Hawaii).

MATERIAL EXAMINED.—Lectotype ♂, Hawaii, Kilauea. Maui: 1♂, Wailua (BPBM). Hawaii: 1♂, paralectotype, same data as lectotype, 1♂, 1 abdomen missing, Kilauea, on *Lythrum* (BPBM); 4♂, Kilauea (BMNH); 4♂, Kealahakua (BMNH).

REMARKS.—This species can be distinguished by its small size (♂, 2.6 mm, ♀, 2.8 mm), stramineous or brown markings on the head (Figs. 5, 7), brown markings on the first thoracic sternite and dorsum of the abdomen, the head being distinctly wider than the pronotum (Figs. 5, 7), 3.3 midtibial setal formula, robust aedeagal shaft (Fig. 24), and the moderately long preapical lobe on the style (Fig. 6).

The medial length of the vertex varies from

slightly longer than to 1.5 times length next to eyes (Figs. 5, 7).

*Balclutha nigriventris*, n. sp.

Figs. 9–11, 19

LENGTH.—♂, 3.0–3.3 mm; ♀, 3.2–3.5 mm.

Yellow to greenish yellow, variably tinged with orange to brown on head, venter, and legs. Dorsum of abdomen dark brown.

External characters as in *fuscifrons*.

MALE.—Genitalia as in *fuscifrons* but with aedeagal shaft curved slightly more dorsally (Fig. 19).

FEMALE.—Genitalia with posterior margin of pregenital sternite more or less straight. Valvulae as in *incisa* (Figs. 33, 38).

HOST.—*Deschampsia* (Gramineae).

DISTRIBUTION.—Endemic (Maui, Hawaii).

HOLOTYPE.—♂, Hawaii: Hualalai, 6,000–7,000', 21.iv.1944, N. L. H. Krauss (BPBM). Paratypes: Maui: 3♂, 3♀, Halemau Trail, 1.v.1945, 8,000' (1♂, on *Deschampsia*); 1♂, Holua, Haleakala Crater, 6,500', vi.1953. Hawaii: 1♂, 1♀, same data as holotype; 1♀, Hualalai, Hinatapoula, 5,900', vii.1964 (BPBM, BMNH).

REMARKS.—This species is similar to *fuscifrons* but is significantly smaller, often lacks the brown marking on the clypellus, and has the shaft of the aedeagus slightly different in shape (compare Figs. 18, 19).

*Balclutha grandis* Namba

Fig. 21

*Balclutha grandis* Namba, 1956: 105–106, Figs. 4a–b. Holotype ♂, Kauai (BPBM) [examined].

HOST.—Unknown.

DISTRIBUTION.—Endemic (Kauai).

MATERIAL EXAMINED.—Holotype ♂, Kauai: Alakai Swamp, viii.1953, 4,000' (BPBM).

REMARKS.—This species can be distinguished by its large size (♂, 4.5 mm, ♀, 5.3 mm), the head being distinctly wider than the pronotum, 4.4 midtibial setal formula, broad stem of the connective, and the shape of the aedeagus (Fig. 21). Namba (1956) recorded 1♂, 1♀ from the type locality.

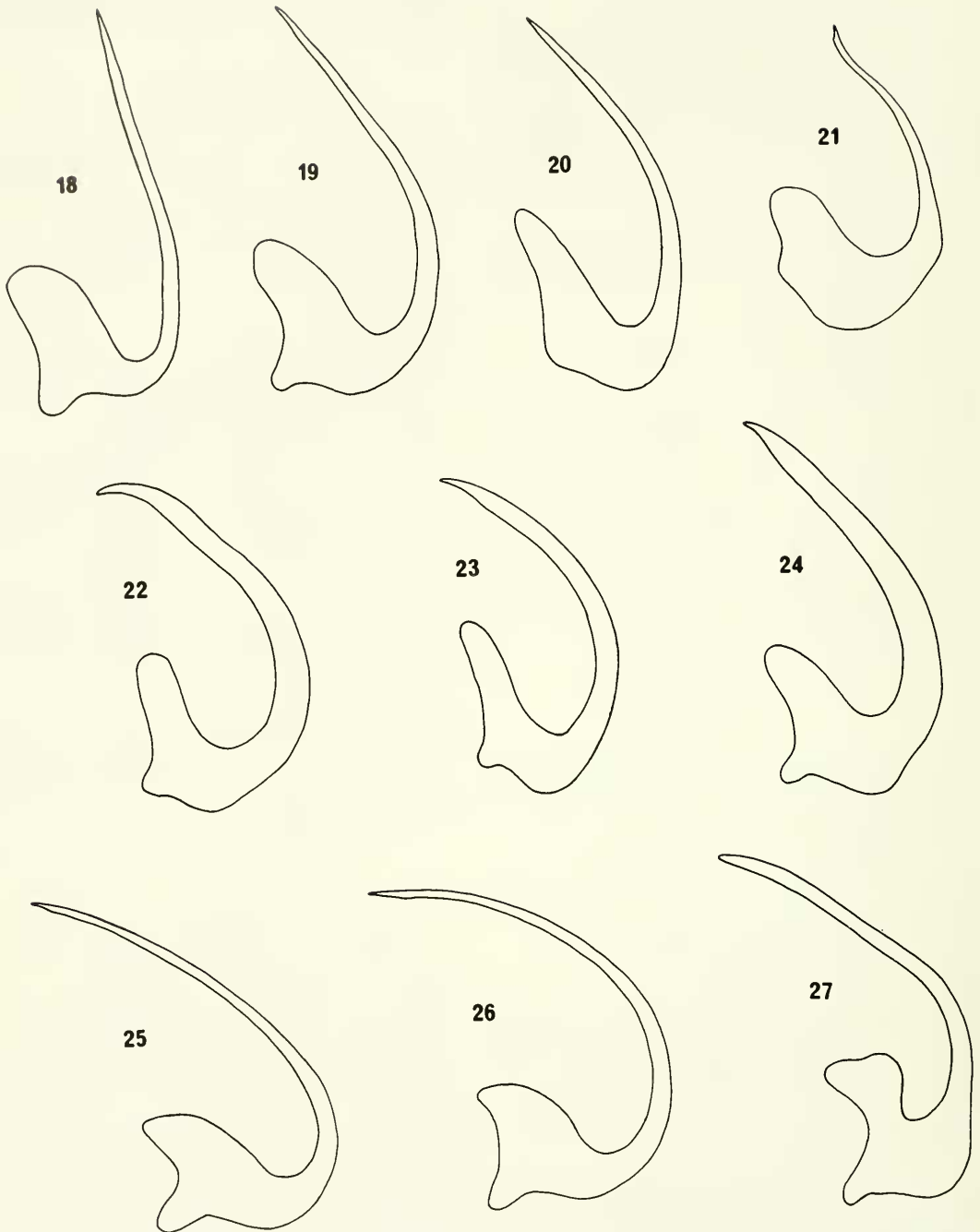
*Balclutha lobata* Namba

Figs. 8, 16, 17, 20

*Balclutha lobata* Namba, 1956: 106, Figs. 5a–b. Holotype ♂, Kauai (BPBM) [examined].

HOST.—*Cyathodes* (Gramineae), *Styphelia* (Epacridaceae).





Figs. 18–27. Endemic Hawaiian *Balclutha* species, aedeagus, left lateral view. 18, *B. fuscifrons*; 19, *B. nigriventris*; 20, *B. lobata*; 21, *B. grandis*; 22, *B. timberlakei*; 23, *B. phoxocephala*; 24, *B. volcanicola*; 25–26, *B. plutonis*; 27, *B. usitata*.

DISTRIBUTION.—Endemic (Kauai, Oahu, Molokai, Maui, Hawaii).

MATERIAL EXAMINED.—Holotype ♂, Kauai, Kokee, vii. 1952, 3,600' (BPBM). Kauai: 8♂,

4♀, Pihea, Kaunuohua Ridge, 4,260'; 6♂, 1♀, Kokee, on *Styphelia*. Molokai: 1♂, Komoku; 9♂, 6♀, above Waikolu V. 1,400m; 1♂, Kalaupapa Lookout; 2♂, Kewala Gulch,

3,500'. Maui: 1♀, Kula Pipe Line, 4, 22' (BMNH, BPBM).

REMARKS.—This species can be distinguished by its moderately large size (♂, 3.0–3.3 mm, ♀, 3.3–3.4 mm), its dark appearance resulting from the dark brown dorsum of the abdomen and the greenish tinge of the forewings, the 3.3 midtibial setal formula, the disc of the female pregenital sternite marked with brown (Fig. 8), and the large preapical lobe of the style (Fig. 16). Some specimens (Molokai) have the lobe of the style narrower (Fig. 17). Contrary to Namba (1956), the head is approximately equal in width to the pronotum.

*Balclutha plutonis* (Kirkaldy)

Figs. 25, 26

*Nesosteles plutonis* Kirkaldy, 1910: 574; Osborn 1935: 57–58, Fig. 24d. Lectotype ♂, Hawaii, here designated [examined].

*Balclutha plutonis* (Kirkaldy): Zimmerman 1948: 87, Fig. 27, Namba 1956: 105, Fig. 3.

HOST.—*Coprosma* (Rubiaceae), *Vaccinium reticulatus* (Ericaceae), *Sophora* (Leguminosae), *Argyroxiphium virescens*, *Raillardia* (Compositae), *Deschampsia*, *Eragrostis* (?) (Gramineae), *Vincentia* (Cyperaceae).

DISTRIBUTION.—Endemic (Maui, Hawaii).

MATERIAL EXAMINED.—Lectotype ♂, Hawaii, Kilauea, vii.1906, R. C. L. Perkins (BPBM). Numerous specimens from Maui (Haleakala, Puu Luau, Puu Noaiuau) and Hawaii (Pohakuloa, Kilauea, Mauna Loa, Hualalai) (BPBM, BMNH).

REMARKS.—This species can be distinguished by its moderately large size (♂, 3.5–3.6 mm, ♀, 3.6–4.0 mm), its uniform yellow or greenish yellow color, usually without brown markings on dorsum of abdomen, and the elongate, evenly curved shaft of the aedeagus. It is similar to *peregrina* but is larger, has the shaft of the aedeagus usually slightly longer, the connective longer than rather than equal in length to the styles, and the sides of the clypellus concave rather than straight. The lectotype is the only specimen known to have the dorsum of the abdomen brown and a slightly shorter aedeagal shaft (Fig. 25), similar to *peregrina*. The setal formulae vary as follows: foretibia, 1.3, 1.4, or 1.5; midtibia, 4.4 or 5.4; hind femur, 2.1.1 or 2.1.1.1.

*Balclutha peregrina* (Kirkaldy)

Fig. 12

*Nesosteles peregrina* Kirkaldy, 1910: 575. Holotype ♂, Hawaii (BPBM) [examined].

*Balclutha peregrina* (Kirkaldy): Zimmerman 1948: 86–87, Fig. 27, Namba 1956: 108, Figs. 8a–c.

HOST.—*Cyathodes*, *Deschampsia* (Gramineae), *Raillardia* (Compositae), *Vaccinium* (Ericaceae), *Styphelia* (Epacridaceae).

DISTRIBUTION.—Endemic (Maui, Hawaii).

MATERIAL EXAMINED.—Holotype ♂, Hawaii: Kilauea, vi.1903, R. C. L. P. Hawaii: (numerous specimens from Kilauea); 2♂, 5♀, Stainback Highway, 2,134 m, on *Styphelia* (BPBM, BMNH).

REMARKS.—This species is similar to *plutonis* but is significantly smaller (♂, 2.6–3.1 mm; ♀, 2.8–3.1 mm), has the abdomen sometimes marked with pale brown, the sides of the clypellus straight (Fig. 12), and the midtibial setal formula 4.3 or 4.4. A few specimens examined (Stainback Highway) are tinged with scarlet and have the abdomen and thoracic sternites marked with dark brown.

*Balclutha usitata* Namba

Fig. 27

*Balclutha usitata* Namba, 1956: 104–105, Figs. 2a–b. Holotype ♂, Kauai (BPBM) [examined].

HOST.—*Cyathodes* (Gramineae).

DISTRIBUTION.—Endemic (Kauai, Oahu, Molokai, Maui, Hawaii).

MATERIAL EXAMINED.—Holotype ♂, Kauai, Kainamanu, vii.1952, 3,800' (BPBM). Numerous specimens from throughout its range (BMNH, BPBM).

REMARKS.—This species can be distinguished by its small size (♂, 2.6–2.9 mm, ♀, 2.8–3.1 mm), its overall yellow or greenish yellow color without brown markings on the dorsum of the abdomen, the 3.3 midtibial setal formula, and the angularly curved aedeagal shaft (Fig. 27). Some specimens have stramineous markings similar to but paler than in *volcanicola* (Figs. 5, 7).

*Balclutha timberlakei* (Osborn)

Figs. 13–15, 22

*Nesosteles timberlakei* Osborn, 1935: 59–60, Figs. 25a–d. Holotype ♂, Oahu (BPBM) [examined].

*Balclutha timberlakei* (Osborn): Zimmerman 1948: 87, Figs. 7e, 24c; Namba 1956: 108–109, Figs. 9a–b.

HOST.—*Eragrostis variabilis* (Gramineae).

DISTRIBUTION.—Endemic (Kauai, Oahu,

Molokai, Lanai, Maui, Hawaii).

MATERIAL EXAMINED.—Holotype ♂, Oahu (BPBM). Oahu: 1♂ (paratype) Palolo Val. on *Eragrostis variabilis* (BMNH). Maui: 1♂, Waikapu Val. (BPBM). Hawaii: 1♂, 2♀, Po-hakuloa, 1,800 m (BPBM).

REMARKS.—This species can be distinguished by its small size (♂, 3.0 mm, ♀, 3.4 mm), elongate head that is distinctly wider than the pronotum (Fig. 15), general yellow color without brown markings on the dorsum of the abdomen, 3.3 midtibial setal formula, robust and slightly sinuate shaft of the aedeagus (Fig. 22), and its elongate connective, which is longer than the style (Figs. 13, 14).

*Balclutha phoxocephala* Namba

Fig. 23

*Balclutha phoxocephala* Namba, 1956: 109, Fig. 10. Holotype ♂, Kauai (BPBM) [examined].

HOST.—*Cyathodes*, *Eragrostis variabilis* (Gramineae).

DISTRIBUTION.—Endemic (Kauai, Oahu, Molokai).

MATERIAL EXAMINED.—Holotype ♂, Kauai: Nualolo, viii.1925, on *Cyathodes* (BPBM). Kauai, Oahu, Molokai (9♂, 5♀, paratypes, BPBM).

REMARKS.—This species can be distinguished by its small size (♂, 2.4–2.6 mm, ♀, 2.7–3.0 mm), 3.3 midtibial setal formula, and robust aedeagus (Fig. 23). Some specimens have stramineous markings similar to but paler than in *volcanicola*.

A series of specimens from Hawaii, Pohakuloa, 6,300' (BPBM), may be this species but have the aedeagal shaft more robust.

*Balclutha incisa hospes* (Kirkaldy), n. stat.

Figs. 28–40

*Nesosteles hebe* var. *hospes*, Kirkaldy, 1910: 574; Osborn 1935: 57, Figs. 24a–b. Lectotype ♀, Hawaii (BPBM), designated by Zimmerman (1948: 85) [examined].

*Nesosteles hospes* Timberlake, 1918: 381.

*Balclutha hospes* (Kirkaldy): Zimmerman, 1948: 85, Fig. 24b, Namba 1956: 107, Figs. 6a–b.

HOST.—*Chloris radiata*, *Panicum purpurascens* (Gramineae).

DISTRIBUTION.—Cosmopolitan and throughout the Hawaiian islands.

MATERIAL EXAMINED.—Lectotype ♀ of *Nesosteles hebe* var. *hospes*, Hawaii: Kauai (BPBM). Numerous specimens from Kauai, Oahu, Molokai, and Hawaii (BPBM, BMNH).

REMARKS.—This subspecies can be distinguished by the head being slightly wider than the pronotum, the short vertex (Fig. 28), the ocelli being only 1.0–1.5 times their own diameter from the corresponding eye, the coronal suture visible in facial view (Fig. 29), distinctively shaped aedeagus (Figs. 39, 40), and the brown markings on the female pregenital sternite (Fig. 36). It is similar in external appearance to *B. saltuella* (see REMARKS under *saltuella*).

This subspecies, which occurs in Hawaii, the Marquesas Islands, and the Americas, differs from the nominate subspecies in the Old World by the more laterally directed ventral process of the aedeagus. This distinction suggests that the species may have reached Hawaii from the Americas rather than the Pacific. Contrary to Timberlake's data (1918), the shape of the pygofer process (Fig. 37) is similar but variable in both subspecies.

*Balclutha saltuella* (Kirschbaum)

Figs. 41–46

*Jassus* (*Thamnotettix*) *saltuellus* Kirschbaum, 1868: 86. Holotype ♀, Germany (Museum Wiesbaden) [examined].

*Balclutha beardsleyi* Namba, 1956: 110, 112, Figs. 11a–b. Holotype ♂, Hawaii (BPBM) [examined], syn. nov.

HOST.—Unknown in Hawaii; elsewhere: *Agrostis* (Gramineae) and *Gossypium* (Malvaceae) (Knight 1987).

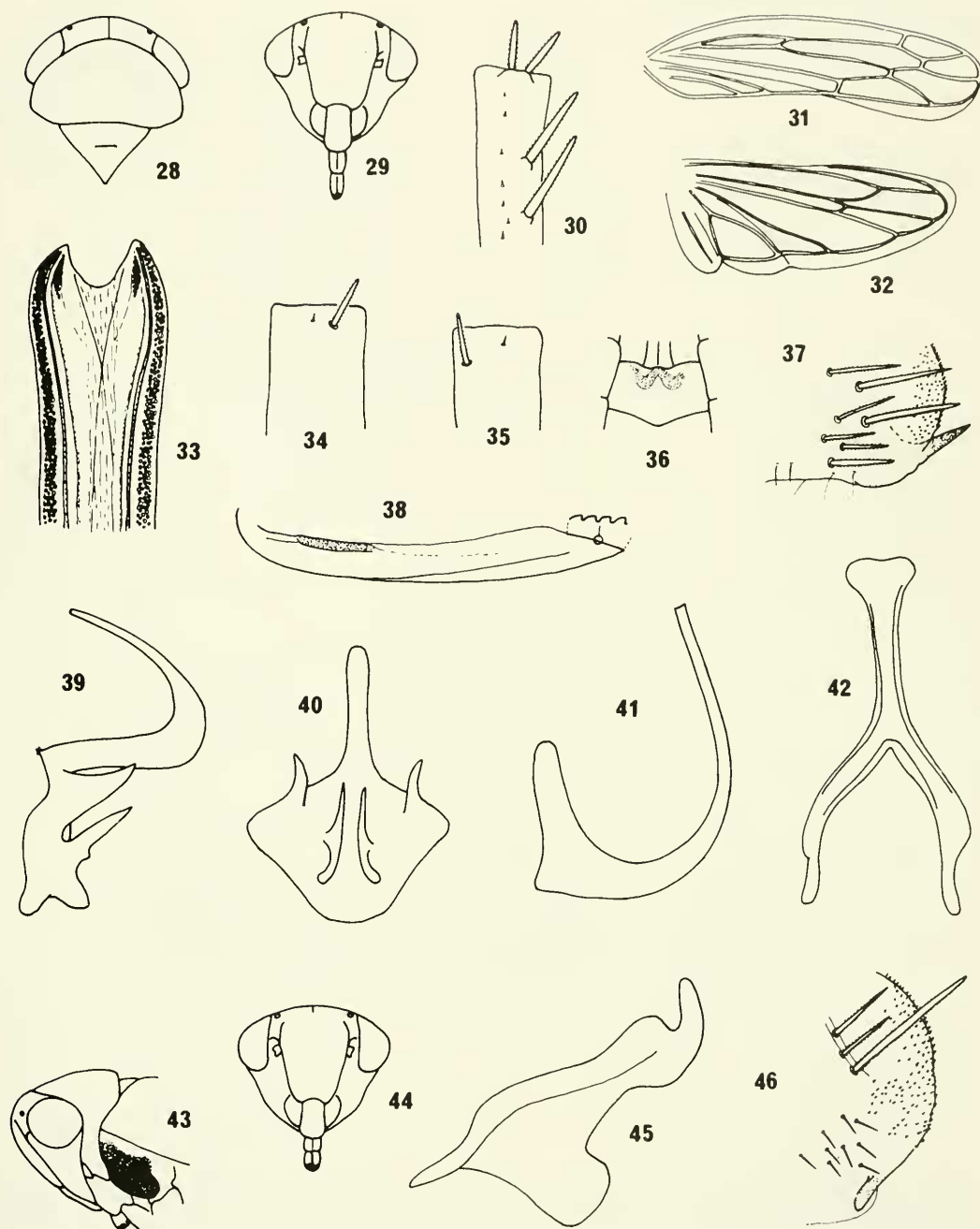
DISTRIBUTION.—Cosmopolitan and on Oahu.

MATERIAL EXAMINED.—Holotype ♀ *Jassus* (*Thamnotettix*) *saltuellus*, Germany (Museum Wiesbaden). Holotype ♂ *B. beardsleyi*, Oahu: Honolulu, i.1955 (BPBM). Oahu: 1♂, 3♀, Honolulu; 1♀, Ewa (BPBM).

REMARKS.—This species is similar to *B. incisa* in external appearance but differs from this and other Hawaiian species by its reduced number of foretibial spines (1.1), its medially directed, lateral frontal sutures, and the short, broad rostrum in facial view (Fig. 44). It differs from *incisa*, in addition, by having the prosternum dark brown (Fig. 43), the female pregenital sternite with a medial, triangular lobe on the posterior margin, and the disc devoid of brown markings.

*Nesolina* Osborn

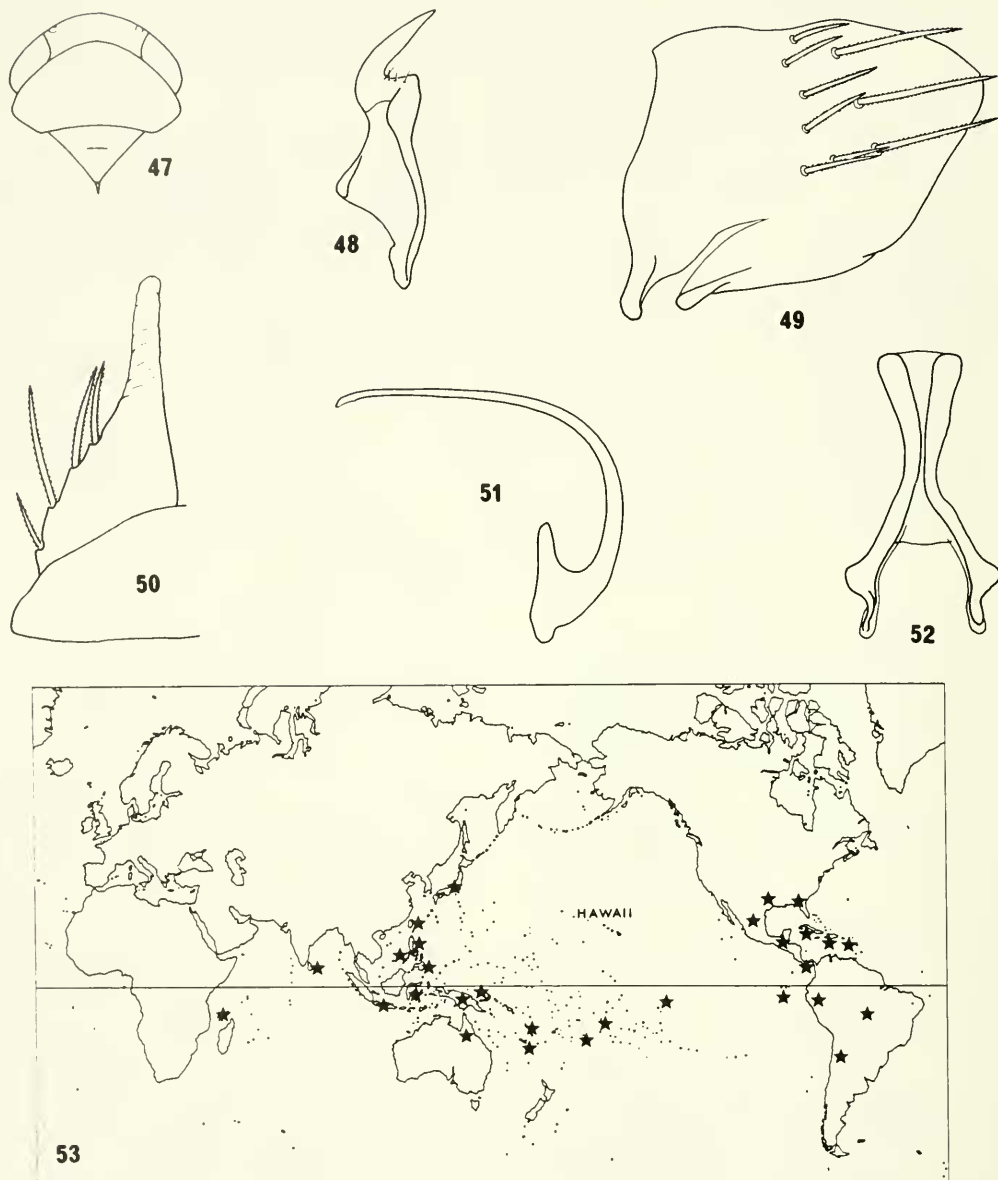
*Nesolina* Osborn, 1935: 60. Type species: *Nesolina lineata* Osborn, by original designation: Zimmerman 1948: 87.



Figs. 28–46. *Balclutha* species. 28–40, *B. incisa hospes*: 28, head and thorax, dorsal view; 29, face; 30, apex of left hind femur; 31, right forewing; 32, right hindwing; 33, apex of second valvulae, ventral view; 34, apex of left midtibia; 35, apex of left foretibia; 36, female pregenital sternite; 37, ventroposterior corner of male pygofer lobe, lateral view; 38, left second valvula, lateral view (toothed area between broken lines); 39, aedeagus, left lateral view; 40, aedeagus, posterior view. 41–46, *B. saltuella*: 41, aedeagus, left lateral view; 42, connective, dorsal view; 43, head and thorax, left lateral view; 44, face; 45, right style, dorsal view; 46, posteroventral corner of male pygofer lobe.

REMARKS.—This endemic Hawaiian genus can be distinguished by its long head and distinctive markings, its large aedeagus with-  
out out processes, and the plumose macrosetae of





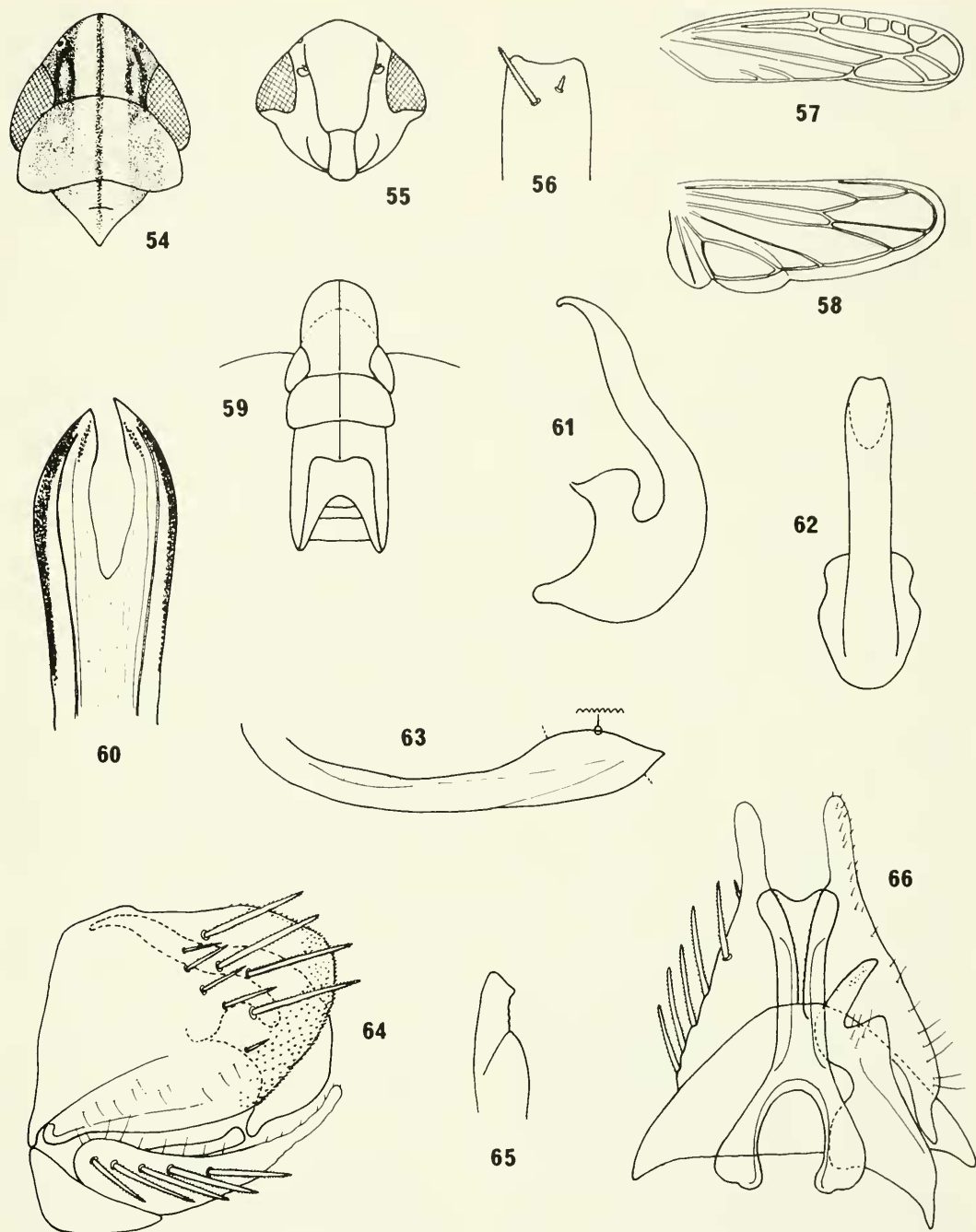
Figs. 47–53. *Balclutha lucida*: 47, head and thorax, dorsal view; 48, left style, dorsal view; 49, male pygofer, left lateral view; 50, left subgenital plate, ventral view; 51, aedeagus, left lateral view; 52, connective, dorsal view; 53, distribution.

the legs and genitalia. The foretibia and midtibia each have one long, and one short, stout apical seta. Setal formulae: foretibia, 1.3; midtibia, 3.3; hind femur, 2.1.1. (see also REMARKS under “Relationship of *Balclutha* to Other Hawaiian Macrostelini”).

### *Nesolina lineata* Osborn

Figs. 54–66

*Nesolina lineata* Osborn, 1935: 60–61, Figs. 26a–c; Zimmerman 1948: 88, Figs. 7d, 8e–f, 24d. Lectotype ♂, Oahu (BPBM), here designated [examined].



Figs. 54–66. *Nesolina lineata*: 54, head and thorax, dorsal view; 55, face; 56, apex of left foretibia; 57, right forewing; 58, right hindwing; 59, immature, head and thorax, dorsal view; 60, apex of first valvulae; 61, aedeagus, left lateral view; 62, aedeagus, posterior view; 63, left second valvula, lateral view (toothed area between broken lines); 64, male genital segment, left lateral view; 65, apex of left style, lateral view; 66, subgenital plates, dorsal and ventral view, valve, connective, and left style, dorsal view.

HOST.—*Eragrostis variabilis* (Gramineae).  
DISTRIBUTION.—Endemic (Oahu, Hawaii).

MATERIAL EXAMINED.—Lectotype ♂, Oahu:  
Diamond Head, 18.ii.1917, W. M. Giffard.

Oahu: 11♂, 8♀, 5 immatures, Diamond Head, various dates (paralectotypes) (BPBM). Hawaii: 1♂, Kau; 1♂, Pohakuloa, on bunch grass (BMNH).

*Balolina*, n. gen.

Type species: *Macrosteles kilaueae* Kirkaldy.

LENGTH.—3.6–4.3 mm.

Yellow to greenish yellow, variably marked with brown. Head slightly to distinctly narrower than pronotum. Vertex triangular, medial length approximately 1.5 times length next to eye, foremargin broad to narrowly parabolic. Ocelli marginal, visible dorsally, situated approximately midway between eye and midline. Face slightly wider than long, lateral margin strongly sinuate below eye. Clypeus narrow, lateral margins incurved at level of eye. Transclypeal suture indistinct. Clypellus narrow, slightly expanded to near apex, extended well beyond margin of face. Laterofrontal sutures extending one-half distance to corresponding ocellus. Pronotum 1.5 times length of vertex, lateral margins short. Forewings elongate, appendix wide, extending around first and second apical cells; outer subapical cell absent; inner subapical cell open basally. Hindwing with veins r and m fused distally. Forefemora with two stout apical setae. Foretibia setal formula 1.3. Midfemora with one long, and one moderately long, stout apical seta. Midtibia setal formula usually 3.3. Hind femora setal formula usually 2.2.1. Base of hind tarsomere sulcate.

MALE.—Pygofer narrowly rounded posteriorly; a group of submarginal macrosetae posteriorly. Subgenital plates gradually tapered to lightly sclerotized, fingerlike apex; a multiserial row of macrosetae along ventrolateral margin. Styles with apical process tapered to acute apex in ventral view, apex footlike in medial view; lateral lobe well developed; inner basal apophyses short. Connective Y-shaped; stem short, equal in length to arms; articulating with aedeagus. Aedeagus with shaft short and robust, cylindrical; a pair of short processes apically; gonopore apical on ventral surface; basal apodeme short.

FEMALE.—First valvulae fused. Second valvulae evenly tapered to acute apex; teeth very fine, extending over distal half of dorsal margin and onto apex of ventral margin.

REMARKS.—This genus is similar in appear-

ance to *Balclutha* and *Nesochlutha* but can be distinguished from these genera by the absence of hairy macrosetae, shorter laterofrontal sutures, indistinct transclypeal suture, the ocelli situated more distant from the eyes, the subgenital plates with multiserial macrosetae, and the aedeagus with a pair of apical processes. It differs from *Balclutha* also by the other characters noted in the key.

*Balolina kilaueae* (Kirkaldy), n. comb.

Figs. 67–83

*Macrosteles kilaueae* Kirkaldy, 1910: 575. Holotype ♀, Hawaii (BPBM) [examined].

*Balclutha kilaueae* (Kirkaldy): Zimmerman 1948: 86, Figs. 7a, 11d–f; Namba 1956: 103–104, Figs. 1a–b.

HOST.—*Cibotium chamissoi* and *C. menziesii* (Dicksoniaceae) (ferns).

DISTRIBUTION.—Endemic (Kauai, Oahu, Molokai, Maui, Hawaii).

MATERIAL EXAMINED.—Holotype ♀, Hawaii, Kilauea, vii. 1906, RCL Perkins. Numerous specimens from throughout its range (BPBM, BMNH).

REMARKS.—The specimens examined varied in color and in the length of the vertex. Brown markings are often present on the dorsal and ventral surfaces of the abdomen and sometimes on the thorax, the clypeus, the basal two-thirds of the ovipositor, the basal half of the corium of the forewing, and the hind legs. One specimen examined from Maunawainui Valley, Molokai, has the clavus of the forewing pale scarlet. Setal formulae: foretibia, 1.3; midtibia, usually 3.3 but sometimes 4.3, 4.4, or 5.3; hind femur, usually 2.2.1, sometimes 2.1.1.1, 2.2.1.1, or 2.1.2.1.1.

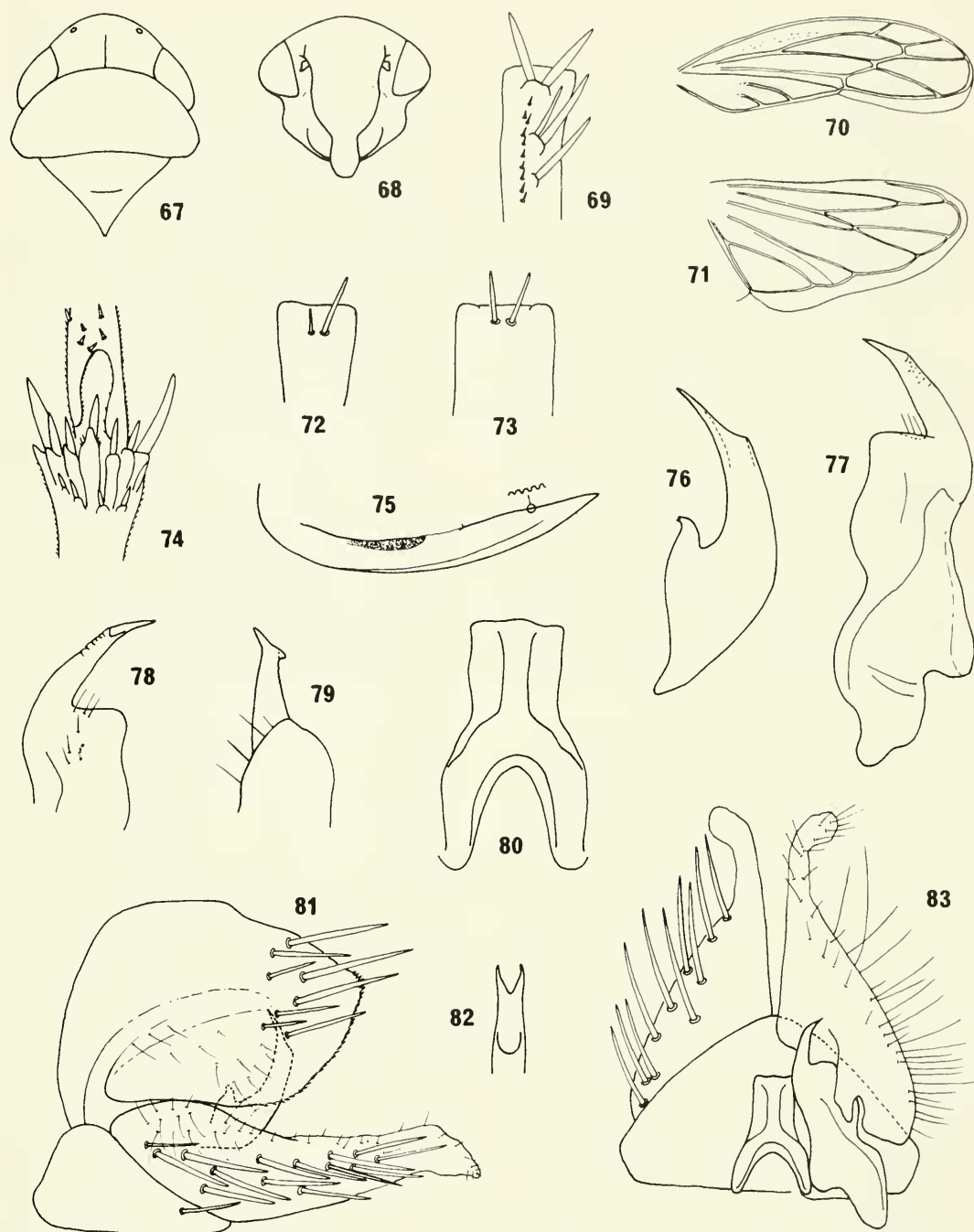
This species is similar in external appearance to *Balclutha nambai* with which it may be confused.

ACKNOWLEDGMENTS

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LITERATURE CITED

- BLOCKER, H. D. 1967. Classification of the Western Hemisphere *Balclutha* (Homoptera: Cicadellidae). Proceedings of the United States National Museum 122: 1–55.  
FABRICIUS, J. C. 1775. Systeme Entomologiae. Flensburgi et Lipsiae, xxviii + 832 pp.



Figs. 67–83. *Balolina kilaueae*: 67, head and thorax, dorsal view; 68, face; 69, apex of left femur; 70, right forewing; 71, right hindwing; 72, apex of left midtibia; 73, apex of left foretibia; 74, apex of hind tibia and base of first tarsus; 75, left second valvula, lateral view (toothed area between broken lines); 76, aedeagus, left lateral view; 77, right style, dorsal view; 78–79, apex of right style, ventral and medial view; 80, connective, dorsal view; 81, male genital segment, left lateral view; 82, apex of aedeagus, posterior view; 83, subgenital plates, dorsal and ventral view, valve, connective, and left style, dorsal view.

FIEBER, F. X. 1866. Neue Gattungen und Arten in Homoptern (Cicadina Bur.). Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien 16:

497–516.

GHAURI, M. S. K. 1966. Revision of the genus *Orosius* Distant (Homoptera: Cicadelloidea). Bulletin of



- the British Museum (Natural History) Entomology 18: 231-252.
- KIRKALDY, G. W. 1900. Bibliographical and nomenclatural notes on the Rhynchota. No. 1. Entomologist 33: 238-243.
- . 1910. Fauna Hawaiiensis 2: 531-700.
- KIRSCHBAUM, C. L. 1868. Die Cicadinen der Gegend von Wiesbaden und Frankfurt a.M. nebst einer Anzahl neuer oder schwer zu unterscheidender Arten aus anderen Gegenden Europas. Jahrbuch des Nassauischen Vereins für Naturkunde 21-22: 1-202.
- KNIGHT, W. J. 1987. Leafhoppers of the grass-feeding genus *Balclutha* (Homoptera, Cicadellidae) in the Pacific region. Journal of Natural History 21: 1173-1224.
- LINNAVUORI, R. 1960. Cicadellidae (Homoptera, Auchenorrhyncha) of Fiji. Acta Entomologica Fennica 15: 1-70.
- NAMBA, R. 1956. A revision of the *Balclutha* species found in Hawaii, with descriptions of five new species (Homoptera: Cicadellidae). Proceedings of the Hawaiian Entomological Society 16: 101-112.
- OMAN, P. W. 1949. The Nearctic leafhoppers (Homoptera: Cicadellidae). A generic classification and check list. Memoirs of the Entomological Society of Washington No. 3: 1-253.
- OSBORN, H. 1935. Cicadellidae of Hawaii. Bulletin Bernice P. Bishop Museum 134: 1-62.
- OSSIANNILSSON, F. 1983. The Auchenorrhyncha (Homoptera) of Fennoscandia and Denmark. Part 3: the family Cicadellidae: Deltocephalinae, catalogue, literature and index. Fauna Entomologica Scandinavica 7: 594-981.
- SIMON, C. 1987. Hawaiian evolutionary biology: an introduction. Trends in Ecology and Evolution 2: 175-229.
- SOUTHWOOD, T. R. E. 1978. Ecological methods. Chapman & Hall, London. 524 pp.
- TIMBERLAKE, P. H. 1918. Note on the non-identity of a common Hawaiian jassid with *Nesosteles hebe* Kirkaldy of Fiji. Proceedings of the Hawaiian Entomological Society 3: 381.
- TRIPLEHORN, B. W., AND L. R. NAULT. 1985. Phylogenetic classification of the genus *Baldulus* (Homoptera: Cicadellidae), and notes on the phylogeny of the Macrostelini. Annals of the Entomological Society of America 78: 291-315.
- WEBB, M. D. 1980. The Cicadellidae from Aldabra, Astove and Cosmoledo atolls collected by the Royal Society Expedition 1967-68 (Hemiptera, Homoptera). Journal of Natural History 14: 829-863.
- . 1986. Sugar-cane cicadellids of the genus *Yamatotettix* (Homoptera: Auchenorrhyncha). Journal of Natural History 20: 131-141.
- . 1987. The endemic Macrostelini of the island of St. Helena (Homoptera, Cicadellidae). Revue de Zoologie Africaine 100: 453-464.
- ZIMMERMAN, E. C. 1948. Insects of Hawaii. Vol. 4. Homoptera: Auchenorrhyncha. University of Hawaii Press, Honolulu. 268 pp.